JOURNAL OF CRUSTACEAN BIOLOGY, 29(4): 516-522, 2009

GROWTH AND REPRODUCTION OF THE INTERTIDAL DOTILLID CRAB *ILYOPLAX DESCHAMPSI*

Yasuhisa Henmi and Hiroaki Koga

(YH, correspondence, henmi@gpo.kumamoto-u.ac.jp) Aitsu Marine Station, Center for Marine Environment Studies, Kumamoto University, Matsushima Kami-Amakusa, Kumamoto 861-6102, Japan;
(HK) Graduate School of Science and Technology, Kumamoto University, Kurokami, Kumamoto 860-8555, Japan

ABSTRACT

Growth and reproduction of the intertidal dotillid crab *Ilyoplax deschampsi* were studied in the Ariake Sea, Japan, and life history traits were compared with those of three other species of *Ilyoplax* occurring in temperate regions. New recruits of *I. deschampsi* occurred mainly in July and August, and their carapace widths (CW) were about 2 mm. They grew to 4 mm CW by December, and to 7 mm CW by the following July. Some crabs reached reproductive maturity in the second year of life, but others remained immature until the third year. Most crabs did not survive the third year. The main breeding season was from May to July, which ceased earlier than in other temperate species of *Ilyoplax*. Hepatic and ovarian weights were highest in early May and early June, respectively, and rapidly decreased after August. The earlier breeding of *I. deschampsi* is thought to be an adaptation for avoiding hot, dry habitat conditions during summer.

KEY WORDS: dotillid crab, growth, *Ilyoplax deschampsi*, reproduction, size-frequency distributions

DOI: 10.1651/08-3108.1

INTRODUCTION

The genus *Ilyoplax* Stimpson 1858 (Dotillidae) contains 26 species (Ng et al., 2008) that are common inhabitants of intertidal mud flats in temperate to tropical Indo-West Pacific regions (Kitaura and Wada, 2006). There are four temperate species of *Ilyoplax* in Japan, Korea, and northern China; viz., *I. pusilla* (de Haan, 1835), *I. deschampsi* (Rathbun, 1913), *I. pingi* Shen, 1932, and *I. dentimerosa* Shen, 1932. Ecological studies have concentrated on *I. pusilla*, and there is much less information available on the other three species except for the following: geographical distribution (Wada et al., 1992) and feeding assemblage formation (Kosuge, 1999) of *I. deschampsi*, vertical zonation in the intertidal area (Koh and Shin, 1988), population dynamics and reproductive biology (Wada et al., 1996), and bioconstructor capabilities (Wada, 1994; Wada et al., 1994) of *I. pingi* and *I. dentimerosa*. There are no available data on the population and reproductive biology of *I. deschampsi*.

Ilyoplax deschampsi occurs in the Yellow Sea and the northern part of the Ariake Sea, Japan (Sakai, 1976). This species occurs primarily on silt mud bottoms in upper estuarine areas inundated by brackish water at high tide (Kosuge, 1999). Like most Ocypodoidea inhabiting intertidal mudflats, *I. deschampsi* lives in isolated burrows dug in intertidal areas and forages in the vicinity of burrow openings during daytime low tides. They feed on organic matter in surface mud, which is scooped into the buccal cavity by the chelae. In the buccal cavity, food is sorted from mud after mixing with water from the gill chambers (Grahame, 1983).

Mating occurs in a plugged male burrow (Henmi, in preparation). The burrow-holding males direct their waving (up-and-down movement of both chelipeds) intensively to the approaching wandering females. Females visit several males' burrows before choosing mating partners. Males, who successfully attract females into their burrows, follow females and plug the burrows with mud clods, keep themselves in the burrows for 1-3 days as a form of mate guarding. After the males emerge from the burrows, females continue to incubate their broods in the burrows for two or three weeks before releasing the larvae.

In the present study, we describe life history traits of *I. deschampsi* and compare them with those of the other three species of *Ilyoplax* found in temperate regions. We also discuss the adaptive significance of the growth and reproduction patterns of *I. deschampsi*.

MATERIALS AND METHODS

Field studies were carried out from June 1998 to August 2000 on an intertidal mud bank approximately 6.5 km upstream from the mouth of the Yabe River, which is located on the eastern side of the Ariake Sea, central Kyushu, Japan (33°08′N, 130°26′E). Most individuals of *I. deschampsi* occurred in the upper and middle mudflats; whereas some *I. pusilla* occurred in upper sand-mudflats. During the study period, monthly average air temperature was lowest in February 2000 (5.0°C) and highest in August 1998 (28.4°C) (data from Japan Meteorological Agency, Omuta Station). Duration of emersion in the burrow area usually ranged from 5-8.5 h during each tidal cycle, depending on the phase of the moon.

Feeding efficiency of *I. deschampsi* may depend on water availability and food concentration in surface mud because their food is sorted in the buccal cavity after mixing with water. To estimate water content, five surface mud samples (each of ~100 g and collected at 2-3 mm depth) were taken around the burrows at low tide every month from April to November 2000. Water content of each sample was estimated by reweighing samples after drying at 60°C for 3 days. To estimate food availability, five surface mud samples (each of ~100 g and collected at 2-3 mm depth) were taken around the burrows just after tidal emersion every month from April to October 2000. Each sample was dried at 60°C for 3 days and nitrogen content was measured with an elemental analyzer (FISONS Co., Ltd., Model EA-1108).

Immediately following tidal emersion, when few crabs began their excursions (Kosuge, 1999), 10 quadrats (25×25 cm^2 each) were evenly arrayed in the burrow area and excavated to a depth of 15 cm. Excavated sediment was then washed through a 1.0-mm mesh sieve that retained captured crabs. During the breeding season (mainly early summer), females incubate their broods for two or three weeks. To estimate the seasonal fluctuation of breeding activity exactly, sampling every two weeks is required during summer. Crabs were sampled twice per month from late June to early September 1998, April to early October 1999, and monthly from October 1998 to March 1999. We also estimated seasonal variation in percentage of ovigerous females in samples collected semi-monthly from May to October 2000 (except August), and monthly from January to April and in August 2000; to collect these crabs, the quadrats were evenly arrayed in the burrow area and all specimens in the quadrats were captured by carefully removing mud from around the burrows without sieving.

Carapace widths (CW) of crabs from each sampling quadrat were measured to the nearest 0.1 mm using hand calipers or a micrometer under a binocular microscope. Sex and presence of eggs were recorded. Crabs less than 3.0 mm CW were difficult to sex, and this group of smaller crabs was assumed to include equal numbers of males and females.

Growth patterns were determined by graphical analysis of the modal progression of successive size-frequency distributions. Modes in the size-frequency distributions of each sex were distinguished using the FiSAT II ver. 1.2.2 software package (http://www.fao.org/fi/statist/fisoft/fisat/index.htm).

Non-ovigerous females larger than 6.5 mm CW (n = 30) were captured at random in the burrow area semi-monthly or monthly from March to November 2000. Each crab was dissected under a microscope, and hepatic and ovarian weights (as proportions of body weights) were estimated after drying the tissues at 60°C for 3 days. Ovigerous females with recently deposited eggs (n = 30) were captured at random in the burrow area in May 2000. A fine brush was used to remove eggs from the pleopods and into the water; eggs released in this way were counted under a microscope. From each ovigerous female, 10 eggs were taken at random, and the length and width of each was measured using a micrometer under a binocular microscope.

Mating pairs were captured from burrows with new mud plugs from May to June 1999, and their CWs were measured to the nearest 0.1 mm using hand calipers.

Results

Habitat Conditions

Water content fluctuated significantly by season (ANOVA, P = 0.007), and was low from June to August (Fig. 1, upper panel). Nitrogen content also fluctuated significantly by season (ANOVA, $P < 0.001$) and was low from June to September (Fig. 1, lower panel). But the magnitude of declines in the summer period was relatively small.

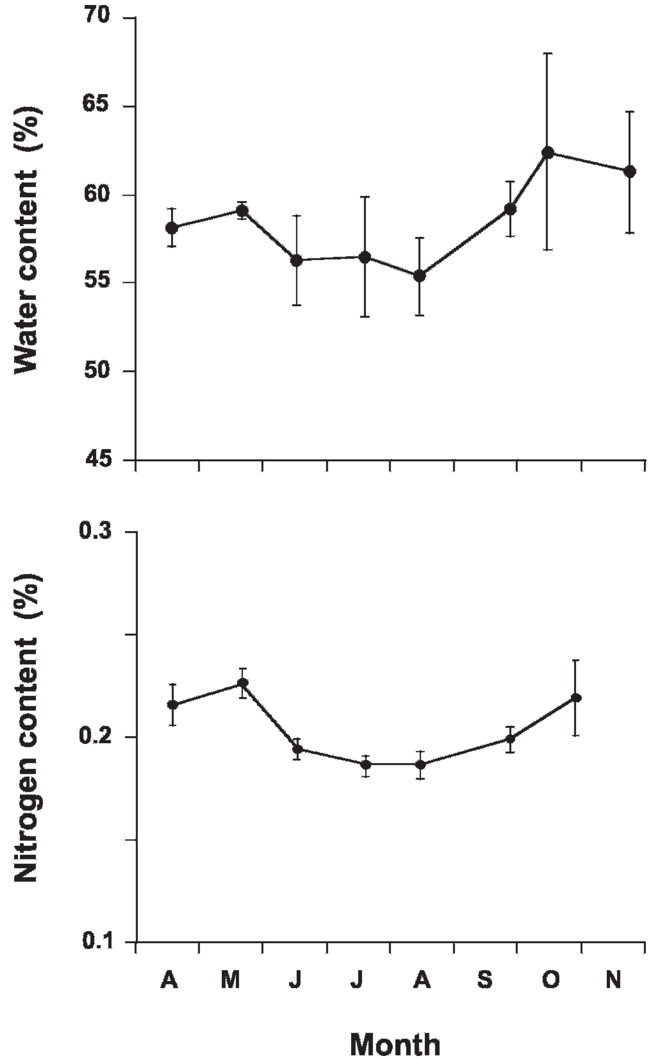

Fig. 1. Water content (upper panel) and nitrogen content (lower panel) of surface mud. Means ± SD, n = 5.

Growth

Ilyoplax deschampsi size-frequency distributions varied from June 1998 to October 1999 (Figs. 2 and 3). Mean crab density fluctuated from 275.2 m^{-2} (late July 1998) to 673.6 m^{-2} (September 1998). Density was high from late August to November in 1998 and from July to September in 1999 when many young crabs were found. The sex ratio remained fairly constant, but there was a female bias in some samples and a significant departure from a 1:1 sex ratio in early August and November 1998 and early April and early May 1999 ($P < 0.05$, Pearson's chi-square test).

It was difficult to detect modes in the size-frequency distributions of the 1996 cohort (individuals hatched in 1996), though some large males and females captured in June 1998 may have been from the 1996 cohort. The 1997 cohort was detected until April or May 1999 and was indistinct thereafter. It is possible that most crabs in the 1997 cohort died before summer 1999. The mean CWs of the 1997 cohort in June 1998 were 5.1 mm in males and 4.6 mm in females, and reached 5.9 mm in males and 5.6 mm in females in September 1998. There was little growth during winter.

The 1998 cohort was present from late July 1998. The mean CW of this cohort was 2.4 mm in late August 1998 when most crabs were difficult to sex, and it increased rapidly to 4.2 mm in males and 4.0 mm in females by December 1998. In 1999, the 1998 cohort grew little until March, but thereafter growth was rapid; the mean CWs were 6.7 mm in males and 6.8 mm in females in early June 1999. Afterward, they grew little and mean CWs reached 7.3 mm and 7.1 mm by October 1999 in males and females, respectively. The 1999 cohort was present from late June 1999 and crabs grew rapidly, reaching mean CWs of 4.2 mm in males and 4.0 mm in females by October 1999.

During the study period (1998-2000), CWs of the largest male and female were 10.8 mm and 10.6 mm, respectively. We estimated growth curves of the 1997 (II), 1998 (III), and 1999 (IV) cohorts (Fig. 4). The growth pattern was almost identical in males and females.

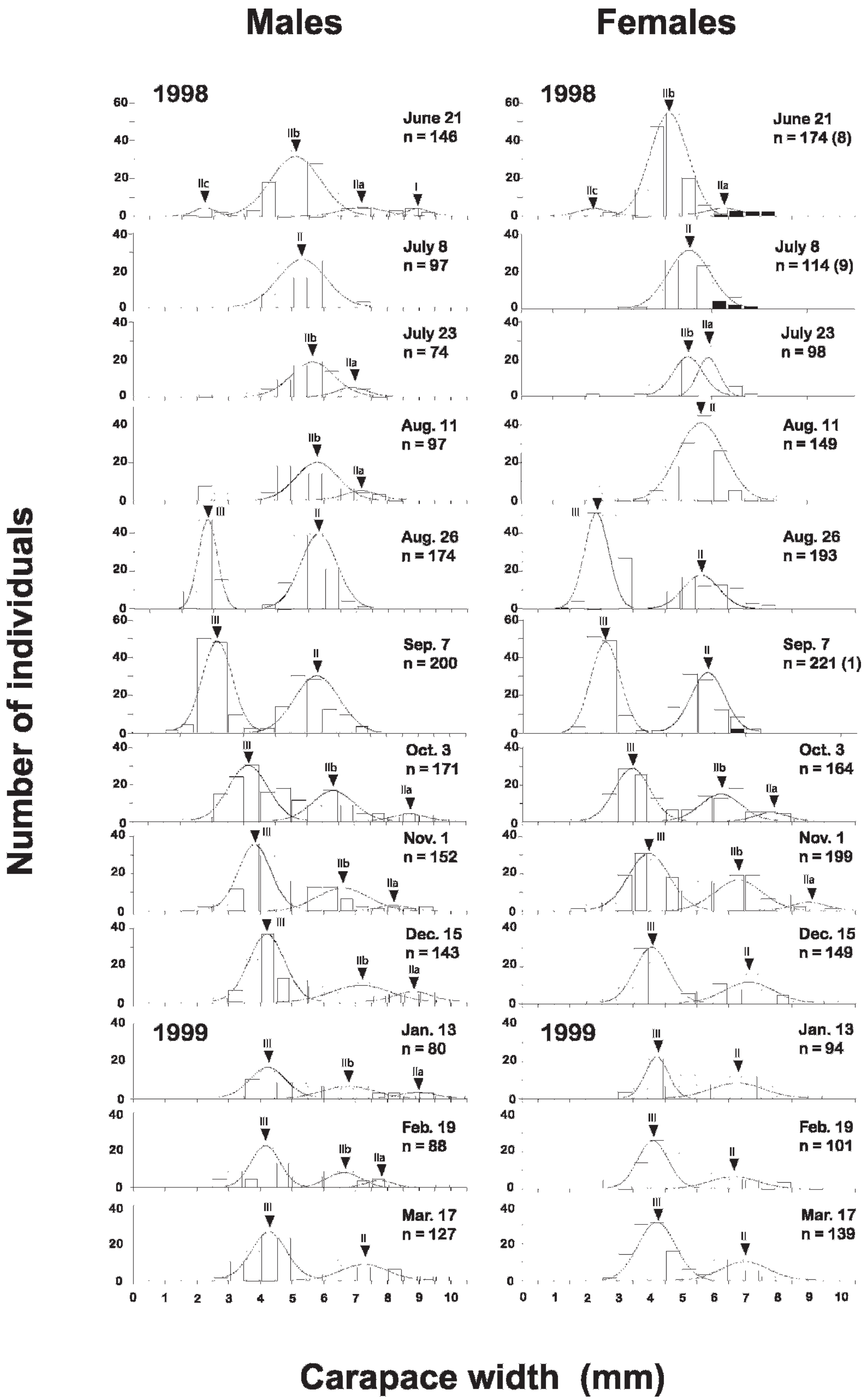

Fig. 2. *Ilyoplax deschampsi*. Size-frequency distributions from June 1998 to March 1999. Black bars indicate ovigerous females. Numbers of ovigerous females are in parentheses. Sexually indeterminate juveniles were assigned genders assuming a sex ratio of 1:1. Roman numbers I, II, III, and IV refer to 1996, 1997, 1998, and 1999 cohorts, respectively. Suffixed lower case letters a, b, and c indicate sub-cohorts within a year cohort.

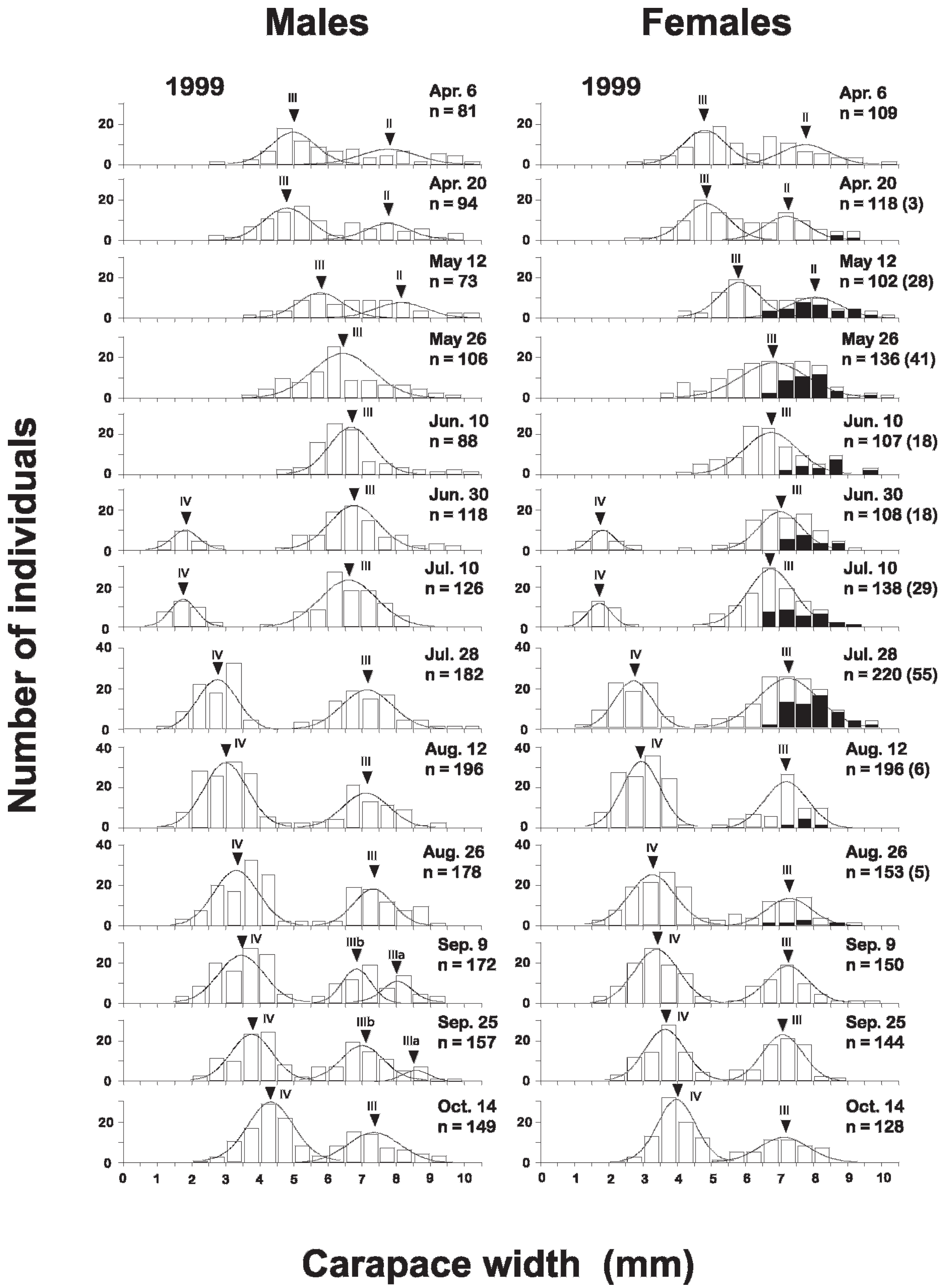

Fig. 3. *Ilyoplax deschampsi*. Size-frequency distributions from April to October 1999. Further details are in the Fig. 2 legend.

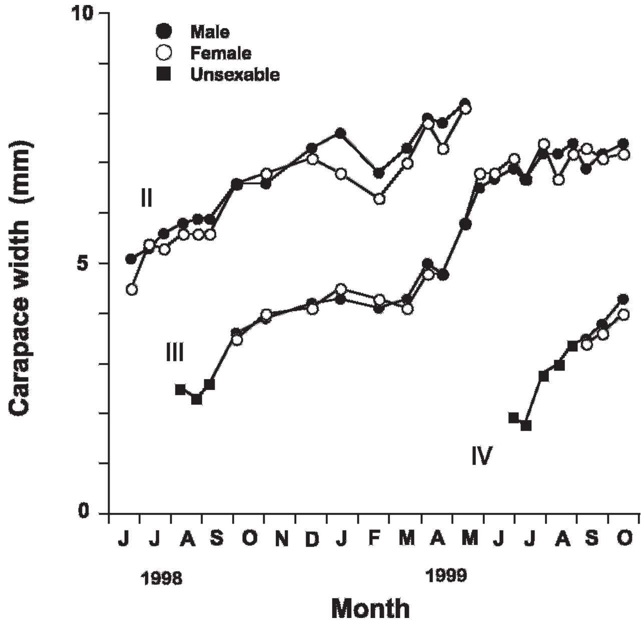

Fig. 4. *Ilyoplax deschampsi*. Estimated growth of the 1997 (II), 1998 (III), and 1999 (IV) cohorts.

Reproduction

The percentage of ovigerous females relative to adult females ($\geq$ 6 mm CW) is shown in Figure 5. Five hundred ovigerous females were captured from 1998 to 2000 (mean CW 8.3 mm, range 6.3-10.6 mm). Ovigerous females occurred from early July through early September in 1998, from late April to late August in 1999, and from late April to mid August in 2000. Few ovigerous females were captured in August 1998 and in September of 1999 and 2000. In each of the years, the percentage of ovigerous females was highest from May to early July.

The log of egg number per brood was significantly correlated with the log of female CW ($P < 0.001$, t test, log $N = 1.196 + 2.490$ log CW, $r = 0.658$, $n = 30$, 7.4-10.8 mm CW). Egg number per brood was 3695 $\pm$ 1204 (mean $\pm$ SD, range 1265-6388, $n = 30$). The mean egg volume was 0.0104 $\pm$ 0.0008 mm^3 and mean diameter was 0.2759 mm $\times$ 0.2655 mm ($n = 10$).

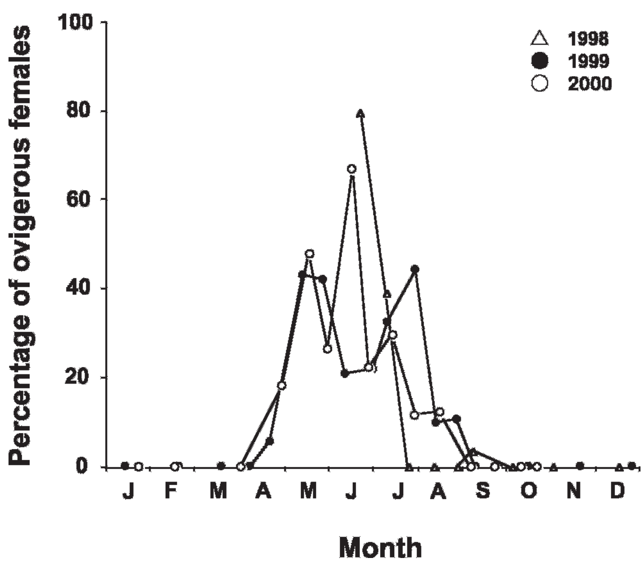

Fig. 5. *Ilyoplax deschampsi*. Seasonal variations in percentage of ovigerous females among adult females over three years.

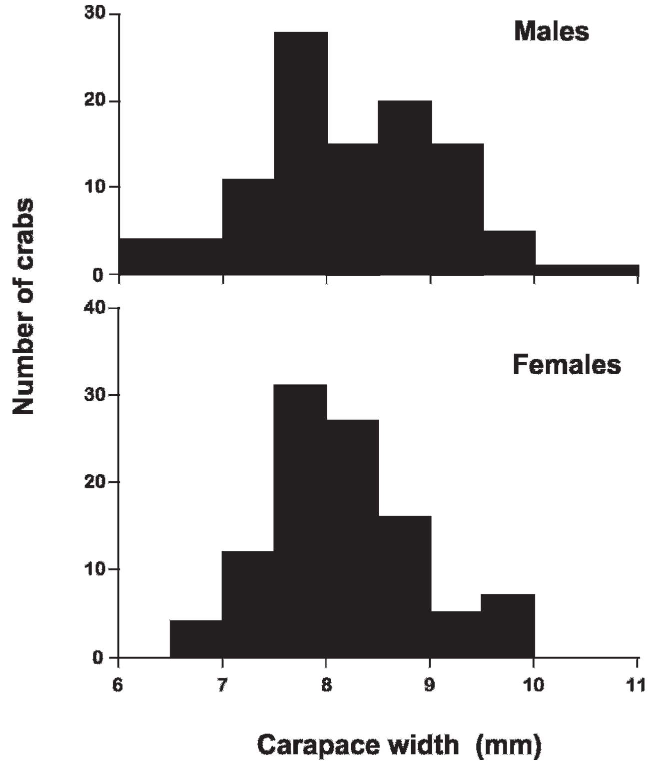

Fig. 6. *Ilyoplax deschampsi*. Size-frequency distributions of male and female crabs in mating pairs ($n = 104$) from May to June 1999.

A total of 104 mating pairs were collected from burrows with new mud plugs. Mean CWs of males and females in mating pairs were 8.2 $\pm$ 0.9 mm (6.3-10.9 mm) and 8.1 $\pm$ 0.8 mm (6.2-10.1 mm), respectively (Fig. 6). There was no significant difference in mean CW (t test, $P > 0.05$) or in size-frequency distribution (Kolmogorov-Smirnov two-sample test, $P > 0.05$) between males and females in mating pairs.

Nutritional Cycles

Hepatic and ovarian weights varied with season (Fig. 7). Hepatic mass was highest in early May (15.7% of body weight), but greatly decreased afterward and stayed at a low level from August to November (2.2-3.7%). Ovary mass was highest in early June (15.1% of body weight), after which it suddenly decreased and stayed at a low level from August to November (0.4-1.3%).

Discussion

Most crabs recruited in July and August following brood production in May or June (this study) and incubation through two or three weeks. Few crabs of the 1996 cohort were collected even in the early part of the study period. The 1997 cohort was detectable until April or May 1999,

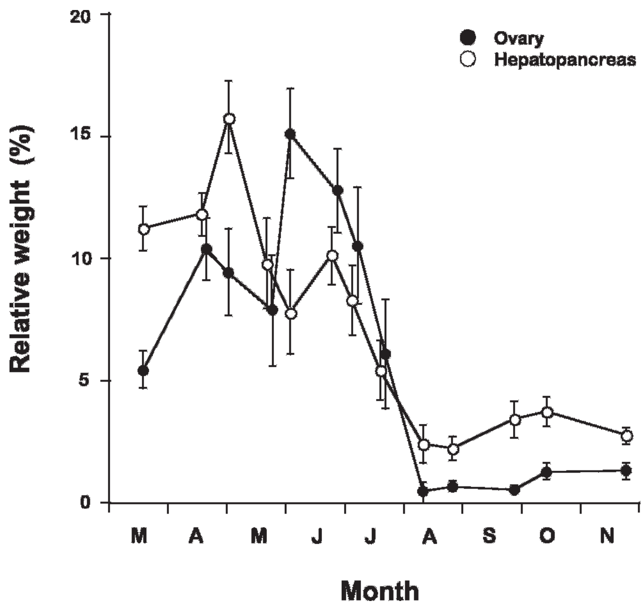

Fig. 7. *Ilyoplax deschampsi*. Seasonal variations in relative weights (% of body mass) of the hepatopancreas and ovary in non-ovigerous females from March to November 2000. Means ± 95% CI, $n = 30$.

but it was barely distinguishable thereafter; it is possible that most crabs of the 1997 cohort died before 1999. Thus, the life span of most *I. deschampsi* may be less than 2 years in the study area. This life span is similar to or slightly shorter than that of *I. pusilla* in northern Kyushu, Japan (Henmi and Kaneto, 1989). The life spans of *I. pingi* and *I. dentimerosa* are unknown.

Most of the mating pairs and ovigerous females were larger than 7 mm CW. However, in the breeding season of their second year, about 50% of crabs were smaller than 7 mm CW. It is reasonable to surmise that many male and female crabs did not breed until their third year, after which they died. In the third year, females may produce 1 or 2 broods (Figs. 2, 3 & 4). The effect of temperature on the incubation period of *I. deschampsi* is unknown, making it difficult to estimate the number of broods per year per female. However, if the incubation period of *I. deschampsi* is similar to that of *I. pusilla* (Henmi and Kaneto, 1989), the number of broods per year per female can be estimated using the equation of Fukui and Wada (1986) to be about 1.7, which is similar to that of *I. pusilla* (1.60) (Henmi and Kaneto, 1989).

During our study, females produced broods mainly from May to July, and few ovigerous females were captured after August. The breeding season is somewhat different from that of other temperate species of *Ilyoplax*. *Ilyoplax pusilla* breeds mainly from June to August in northern Kyushu, Japan (Henmi and Kaneto, 1989) and mainly from April to August in western Kyushu (Takayama, 1996). The main breeding season of *I. pingi* is from June to August; that of *I. dentimerosa* is from April to August (with a marked peak in April and May) in Kanghwa, Korea (Wada et al., 1996). In the latter three species, many females produce broods in August, though the percentage of ovigerous females in April and May was much lower in *I. deschampsi* than in *I. dentimerosa*.

The earlier cessation of breeding in *I. deschampsi* is more obvious in measured ovarian activity. The relative ovarian weight decreased steeply in July, and few females possessed ripe ovaries in August. Relative hepatic mass was also small after August, but the decrease was not as precipitous. Relative hepatic weight decreased in May and ovarian weight increased in early June, which may indicate movement of resources from the hepatopancreas to the ovary. If this is the case, crab activity might have already declined by June and July, although ovarian mass indices were still high in these months. There is no information on ovarian weight seasonal variation in other temperate species of *Ilyoplax*. In *Macrophthalmus banzai* Wada and K. Sakai, 1989 in western Kyushu, Japan, females breed mainly from May to October and ovarian weight is high from April to September (Henmi, 1993).

Breeding periods are determined by a complex interaction of endogenous and exogenous factors, which cause intra- and interspecific variation in duration of reproductive season (Sastry, 1983). Such variations may be a genotypic response to environmental conditions that maximizes reproductive success under favorable conditions. A number of abiotic and biotic factors such as temperature, photoperiod, salinity, and food availability have been identified as major modulators of reproduction in crustaceans (Aiken, 1969; Pillay and Nair, 1971; Snowden et al., 1991; Henmi, 1993; Emmerson, 1994; Company and Sardà, 1997; Litulo, 2005). For example, semiterrestrial brachyuran crab species living in high intertidal zones have a well-defined breeding season that is likely adaptive to severe habitat conditions (Sastry, 1983; Henmi and Kaneto, 1989; Emmerson, 1994; Cobo, 2002).

In *I. deschampsi*, the decline in breeding activity in late summer may be a response to high temperatures and low water content on the mudflat surface (Fig. 1). On drier mud, the crabs cannot feed efficiently because water is required for sorting food from mud (Grahame, 1983). Henmi (1989) reported that summer feeding activity of *Macrophthalmus japonicus* (de Haan, 1835) declined in dry habitats, and some crabs left their burrows and moved to the water's edge forming large feeding assemblages. Such feeding assemblages near the water's edge also occur in *I. deschampsi* at low tide on hot days in July and August (Kosuge, 1999). In *I. dentimerosa*, ovigerous females are most abundant in April, and this may be adaptive in avoiding later hot, dry conditions in the upper intertidal zone where burrow areas are not submerged during neap tides (Wada et al., 1996). Though most parts of *I. deschampsi* habitat were submerged even during high water of neap tides, the exposure duration was prolonged in this part of the lunar cycle, and some burrows in the upper area were not submerged at high neap tide.

The pattern of reproduction was very different between 1998 and 1999 (Fig. 5). There were two equally strong peaks (May and July) in the abundance of ovigerous females in 1999. The interannual variation of reproductive activity may depend on weather conditions. In July 1999, it was very cool and rainy. In July 1998, 1999, 2000, average air temperature was 27.1, 25.4, 27.5°C; precipitation was 204, 252, 127 mm; and sunshine duration was 175.2, 118.4, 214.0 h, respectively (data from Japan Meteorological

Agency, Omuta Station). Under the cool and wet condition, feeding activity may not decline because of low temperature and high water content of the mudflat surface. It may be because many females were ovigerous even in late July 1999. Unfortunately, it is not clear why no female was ovigerous in late July and August 1998. It was not so hot and dry in July 1998.

An alternative explanation for the decline in *I. deschampsi* reproductive activity during late summer may be food shortage; nitrogen content of mud was low during summer (Fig. 1). However, observational data do not disentangle the effects of environmental factors on breeding activity, and experimental manipulations should be undertaken to this end.

Average of egg number and size, and body size of ovigerous females have been reported for other temperate species of *Ilyoplax*: *I. pusilla* (2685 eggs, 0.0127 mm^3, 7.4 mm CW; Henmi and Kaneto, 1989), *I. pingi* (2192 eggs, 0.0112 mm^3, 8.2 mm CW; Wada et al., 1996), *I. dentimerosa* (1135 eggs, 0.0248 mm^3, 8.5 mm CW; Wada et al., 1996). The numbers of eggs in *I. deschampsi* (3695 eggs in 8.3 mm CW female) is the largest of the four temperate species of *Ilyoplax*, and egg size (0.0104 mm^3) is almost identical to those of *I. pusilla* and *I. pingi*, but smaller than that of *I. dentimerosa*. Wada et al. (1996) suggested that the large egg size of *I. dentimerosa* was an adaptation to high temperatures and desiccation stress in the upper intertidal habitat. However, large egg size may be a larval adaptation to habitat, as discussed in many studies (Cobb et al., 1997; Mashiko and Numachi, 2000).

Acknowledgements

We thank Dr. Satoshi Kobayashi for his help with the statistics and two anonymous reviewers for their invaluable commments on the manuscript.

References

Aiken, D. 1969. Ovarian maturation and egg laying in the crayfish *Orconectes virilis*: influence of temperature and photoperiod. Canadian Journal of Zoology 47: 931-935.

Cobb, J. S., J. B. Booth, and M. Clancy. 1997. Recruitment strategies in lobsters and crabs: a comparison. Marine and Freshwater Research 48: 797-806.

Cobo, V. J. 2002. Breeding period of the arrow crab *Stenorhynchus seticornis* from Couves Island, south-eastern Brazilian coast. Journal of the Marine Biological Association of the United Kingdom 82: 1031-1032.

Company, J. B., and F. Sardà. 1997. Reproductive patterns and population characteristics in five deep-water pandalid shrimps in the western Mediterranean along a depth gradient (150–1100 m). Marine Ecology Progress Series 148: 49-58.

de Haan, W. 1835. Crustacea, pp. 25-64. In, P. F. von Siebold (ed.), Fauna Japonica. Müller, Amsterdam.

Emmerson, W. D. 1994. Seasonal breeding cycles and sex ratios of eight species of crabs from Mgazana, a mangrove estuary in Transkei, southern Africa. Journal of Crustacean Biology 14: 568-578.

Fukui, Y., and K. Wada. 1986. Distribution and reproduction of four intertidal crabs (Crustacea, Brachyura) in the Tonda River Estuary, Japan. Marine Ecology Progress Series 5: 513-522.

Grahame, J. 1983. Adaptive aspects of feeding mechanisms, pp. 65-107. In, F. J. Vernberg and W. B. Vernberg (eds.), The Biology of Crustacea, Volume 8. Environmental Adaptations, Academic Press, New York.

Henmi, Y. 1989. Factors influencing drove formation and foraging efficiency in *Macrophthalmus japonicus* (De Haan) (Crustacea: Ocypodidae). Journal of Experimental Marine Biology and Ecology 131: 255-265.

———. 1993. Geographic variations in life-history traits of the intertidal ocypodid crab *Macrophthalmus banzai*. Oecologia 96: 324-330.

———, and M. Kaneto. 1989. Reproductive ecology of three ocypodid crabs, I. The influence of activity differences on reproductive traits. Ecological Research 4: 17-29.

Kitaura, J., and K. Wada. 2006. New species of *Ilyoplax* (Brachyura: Ocypodidae: Dotillinae) from the Philippines and Indonesia: behavioral, molecular, and morphological evidence. The Raffles Bulletin of Zoology 54: 373-379.

Koh, C. H., and H. C. Shin. 1988. Environmental characteristics and distribution of macrobenthos in a mudflat of the west coast of Korea (Yellow Sea). Netherlands Journal of Sea Research 22: 279-290.

Kosuge, T. 1999. Droving in *Ilyoplax deschampsi* (Brachyura: Ocypodidae). Crustacean Reaearch 28: 1-4.

Litulo, C. 2005. External factors determining the reproductive periodicity in a tropical population of the hairy crab *Pilumnus vespertilio* (Decapoda; Brachyura: Pilumnidae). The Raffles Bulletin of Zoology 53: 115-118.

Mashiko, K., and K. Numachi. 2000. Derivation of populations with different-sized eggs in the palaemonid prawn *Macrobrachium nipponense*. Journal of Crustacean Biology 20: 118-127.

Ng, P. K., D. Guinot, and P. J. F. Davie. 2008. Systema brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. The Raffles Bulletin of Zoology 17: 1-286.

Pillay, K. K., and N. B. Nair. 1971. The annual reproductive cycles of *Uca annulipes*, *Portunus pelagicus* and *Metapenaeus affinis* (Decapoda: Crustacea) from the south-west coast of India. Marine Biology 11: 152-166.

Rathbun, M. J. 1913. Description of new species of crabs of the families Grapsidae and Ocypodidae. Proceedings of the United States National Museum 46: 353-358.

Sakai, T. 1976. Crabs of Japan and the Adjacent Seas. Kodansha. Tokyo [In 3 volumes: (1) English text, xxix+773 pp. (2) Plates volume, 16 pp., 251 pls. (3) Japanese text, 461 pp.].

Sastry, A. N. 1983. Ecological aspects of reproduction, pp. 179-270. In, F. J. Vernberg and W. B. Vernberg (eds.), The Biology of Crustacea, Volume 8. Environmental Adaptations, Academic Press, New York.

Shen, C. J. 1932. The Brachyuran Crustacea of North China. Zoologica Sinica, Series A, Invertebrates of China 9: 1-300, 171 text-figs., 10 pls.

Snowden, R. J., A. A. Clayton, and E. Y. Al-Taher. 1991. Population biology of *Ilyoplax stevensi* (Brachyura: Ocypodidae) on a Kuwait mudflat. Marine Ecology Progress Series 71: 219-225.

Stimpson, W. 1858. Prodomus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federate missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observatit et descripsit. V. Crustacea Ocypodoidea. Proceedings of the Academy of Natural Sciences of Philadelphia 10: 93-110.

Takayama, J. 1996. Population structure of *Ilyoplax pusilla* (Crustacea: Ocypodidae) in the Kurae River Estuary, Amakusa, Kyushu, Western Japan. Benthos Research 50: 19-28.

Wada, K. 1994. Earthen structures built by *Ilyoplax dentimerosa* (Crustacea, Brachyura, Ocypodidae). Ethology 96: 270-282.

———, B. L. Choe, J. K. Park, and S. S. Yum. 1996. Population and reproductive biology of *Ilyoplax pingi* and *I. dentimerosa* (Brachyura: Ocypodidae). Crustacean Research 25: 44-53.

———, T. Kosuge, and J. Takayama. 1992. Distribution of *Ilyoplax pusilla* and *I. deschampsi* (Brachyura: Ocypodidae). Researches on Crustacea 21: 139-146. (In Japanese)

———, and K. Sakai. 1989. A new species of *Macrophthalmus* closely related to *M. japonicus* (De Haan) (Crustacea: Decapoda: Ocypodidae). Senckenbergiana Maritima 20: 131-146.

———, S. S. Yum, and J. K. Park. 1994. Mound building in *Ilyoplax pingi* (Crustacea, Brachyura, Ocypodidae). Marine Biology 121: 61-65.

Received: 18 October 2008.
Accepted: 19 January 2009.